

INTERRELATIONSHIPS OF THE TAXINEAE

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(WITH PLATES I, II)

In considering the Taxineae it is interesting to note the taxonomic position to which this subtribe has been assigned at various periods in the history of the classification of the conifers. ENGLER and PRANTL (4) in 1889 placed it at the top of the group; PENHALLOW (6) in 1907 placed it at the bottom of the group; COULTER and CHAMBERLAIN (1) in 1901 regarded the subtribe as the most primitive of the conifers and placed it at the bottom, but in 1910 (2) shifted its position to the top of the group as the most modern. These facts show clearly that the family is a difficult one to interpret, and the difficulty is due in part to the fact that the Taxineae combine at the same time extreme simplification and specialization.

The argument presented by PENHALLOW as evidence for his theory that the Taxineae are the most primitive of the conifers is based on the progressive development of the resin canals in *Pinus* and *Picea* from the isolated resin cells of *Podocarpus* "by various phases of aggregation." In *Taxus* and *Torreya* of the Taxineae, which he investigated, PENHALLOW states that resin cells are entirely wanting. Isolated resin cells occur in abundance in *Podocarpus* of the Taxineae. In the true Coniferae isolated or aggregated resin cells are characteristic of all the genera except *Picea* and *Pinus*, where they are replaced by resin passages, of which the aggregations of resin cells form an essential part. From the genera *Taxus* and *Torreya*, characterized by the absence of resin cells, PENHALLOW traces a series through *Podocarpus*, where resin cells are scattered, to genera of the Coniferae, where first, as in *Taxodium* and *Libocedrus*, the resin cells are arranged in well defined zones as well as scattered, to resin sacs in *Abies* and *Sequoia*, to resin passages with constrictions in the canal in *Larix*, *Pseudotsuga*, and *Picea*, to the resin passages without constrictions, as in *Pinus*.

Those who hold that the Taxineae represent a modern group in the evolution of the conifers interpret the facts already stated in PENHALLOW'S argument as evidence of an entirely different progression. Starting with the genera in which the resin canal is highly specialized and resin cells wholly lacking, as in *Pinus*, they trace a series in which there is a gradual reduction of the resin canal, to aggregations of resin cells as in *Taxodium*, to scattered resin cells as in *Sequoia* and *Podocarpus*, to entire absence of resin cells as in *Taxus*.

As evidence of the fact that resin canals represent a primitive condition in the conifers, JEFFREY'S work on the genus *Sequoia* may be cited. If the presence of resin canals were evidence of modern development, we should expect to find them in the mature and more progressive parts of the plant, but in *Sequoia gigantea* JEFFREY (5) found the resin canals only in the first annual ring in the stem, in the ovulate strobilus, and in the leaf traces of very vigorous leaves of adult trees. In *Sequoia sempervirens* the resin canals were wholly lacking in these regions, but in injured stems and roots of both *S. gigantea* and *S. sempervirens* resin canals were present. In the case of *Sequoia*, then, the presence of resin canals represents a primitive condition in the conifers, retained only in the more conservative regions of the plant in *S. gigantea*, and wholly absent in *S. sempervirens*. A reversion to the ancestral condition in both species may be induced by injury.

According to this later view of the position of the Taxineae as contrasted with that held by PENHALLOW, we have a series of genera starting with *Pinus* as a representative of the most primitive group in which resin canals are normally present, proceeding through *Sequoia* as a type of a group in which resin canals are not normally present in the vegetative axis, until we come to *Podocarpus*, a representative of a group in which resin canals are never present.

In this connection it is important to note that in those groups in which resin canals are normally absent the secretion of resin is carried on by resin parenchyma cells. These resin cells are characteristic of the Taxodineae, Cupressineae, and Podocarpineae. We should expect as the logical outcome of this gradual reduction and simplification of resin secreting structures the final passing out

of the resin parenchyma cells in the more modern types. This question will be taken up later when we consider the genera within the group Taxineae.

Much of the controversy in regard to the position of the Taxineae has been based on the character of the gametophytes and reproductive structures, especially the ovulate cone and the method of development of the proembryo. The evidence which I have to offer is derived wholly from the study of the anatomical structure of the stem and root of various genera in the group.

There are included in the family Taxaceae of ENGLER and PRANTL (4) the genera *Phyllocladus*, *Ginkgo*, *Cephalotaxus*, *Torreya*, and *Taxus*. In the most recent classification of the group by COULTER and CHAMBERLAIN (2) *Phyllocladus* is included in the Podocarpaceae, *Ginkgo* has been put in a family by itself, and the Taxineae include in addition to *Taxus*, *Torreya*, and *Cephalotaxus*, the doubtful New Caledonian genera *Acropyle* and *Poly-podiopsis*. Turning our attention to the 3 accepted genera of the group, *Cephalotaxus*, *Torreya*, and *Taxus*, I shall attempt to show that the Taxineae are the most modern group of the conifers, that *Cephalotaxus* is the most primitive genus of the subtribe and most nearly related to the Podocarpaceae, that *Torreya* is intermediate, and that *Taxus* is the most modern genus of the family and represents, so to speak, the last word in the evolution of the conifers.

If we examine a transverse section of the stem of *Podocarpus totara*, we note the presence in great abundance of resin parenchyma cells (fig. 1). These parenchyma cells are even more evident in the longitudinal section of the stem (fig. 2) as cells which stain densely with haematoxylin due to the presence of resin. These cells are narrower than the tracheids and are characterized by thin walls, by the absence of pits, and end walls at right angles to the long axis of the cell.

A section of the stem of *Cephalotaxus drupacea* (fig. 3) presents a very similar appearance to the stem of *Podocarpus*. That the resin parenchyma cells are widely distributed throughout the annual rings of the stem is evident from a consideration of the low power photograph (fig. 4). The location of these cells is shown by the deep staining of the resinous contents.

The root of *Cephalotaxus drupacea* (fig. 5) shows the presence of resin parenchyma in even greater abundance, and this is the condition we should expect to find, since the root is the more conservative organ of the plant and would retain more fully the primitive or ancestral characteristics of the plant.

The stem of *Torreya taxifolia* presents a very different appearance from the stem of *Podocarpus* and *Cephalotaxus* already considered. Resin parenchyma cells are present throughout the annual ring, but they are much less abundant than in the other stems. The distribution of the cells may be seen in the transverse section (fig. 6), and the character of the cells is shown very clearly in the longitudinal section (fig. 4).

As previously stated, PENHALLOW did not find resin cells in any of the species of *Taxus* or *Torreya* which he investigated, and DEBARY (3) also states that all investigated species of the Coniferae, with the single exception of *Taxus*, have resin passages or resin reservoirs. As a result of my investigation, it is clearly evident that resin parenchyma is present in *Torreya taxifolia*, one of the species investigated by PENHALLOW.

If we examine a transverse section of the stem of *Taxus brevifolia* (fig. 8), we note the complete absence of resin parenchyma cells. A longitudinal section of the same stem (fig. 9) shows even more clearly that the vascular cylinder consists simply of thick-walled tracheids, with numerous bordered pits, and the characteristic spiral thickenings. So far then the condition in *Taxus* tallies with the investigations of PENHALLOW and DEBARY; but if we examine a transverse section of the root of *Taxus cuspidata* (fig. 10) we note the presence of resin parenchyma diffused throughout the annual ring. A higher magnification of a portion of the root is shown in fig. 11. Here the resin parenchyma cells are very conspicuous. A longitudinal view of the same root also shows a view of these parenchyma cells very clearly (fig. 12). The root of *Taxus baccata* also shows the presence of resin parenchyma diffused throughout the annual ring.

Although in the normal stem of the species of *Taxus* investigated there was no resin parenchyma present, a wounded stem of *T. baccata* showed very clearly an extreme development of these cells.

The location of the cells can be determined easily in the transverse section of the stem, due to the fact that the walls stain a deep blue with haematoxylin, and in the longitudinal section the characteristic shape of the parenchyma cells as contrasted with the tracheids make them easily recognizable.

We find then in the normal stem of *Taxus* the condition which we should expect as the ultimate result of the gradual reduction of resin canals, namely, resiniferous parenchyma which finally completely disappears except in the case of conservative organs.

There are three important principles of evolution which have to be considered in working out the ancestry of any group of plants, namely, the principles of recapitulation in the development of the embryo and seedling stages of the plant; retention of ancestral characters in the more conservative regions of the plant, as the root, leaf, and reproductive axis; and reversion to ancestral conditions through injury.

The first of these principles I have not been able to demonstrate, as I did not have access to the seedling stages of the genera investigated. The principle of the retention of ancestral characters in the most conservative organ of the plant is very clearly evidenced in the root of *Taxus cuspidata* by the presence of resin parenchyma cells which have entirely passed out of the stem; and finally the presence in abundance of resin parenchyma in the wounded stem of *Taxus baccata* seems to show clearly that we have in this instance a reversion to the ancestral condition.

From a consideration of these facts the evidence seems to justify the conclusion that the Taxineae are the most modern group of conifers; that of the Taxineae, *Cephalotaxus* is the most primitive, in most nearly resembling *Podocarpus* in the abundance of resin parenchyma; that *Torreya* is the intermediate genus in the group, as shown by the reduction of resin parenchyma, especially in the stem; and that *Taxus* is the most modern genus in the group, since we find here entire absence of resin parenchyma in the stem, although it is retained in the root.

Summary

1. Resin parenchyma is present in abundance in the stem and root of *Cephalotaxus drupacea* and shows clearly its close relationship

to the Podocarpaceae, a family in which resin parenchyma is universal.

2. Resin parenchyma is present in less abundance in the stem of *Torreya taxifolia*, showing in this respect an intermediate position between *Cephalotaxus* and *Taxus*.

3. Resin parenchyma is wholly absent in the normal stem of *Taxus brevifolia*, showing that this genus is the most modern one of the group.

4. Resin parenchyma in the root of *Taxus cuspidata* and *T. baccata* and in the wounded stem of *T. baccata* indicates the ancestral condition in this genus.

5. The Taxineae represent a modern group of conifers, as shown by the gradual reduction and final passing out of resin parenchyma in the more progressive organs.

This investigation was carried on in the laboratories of Plant Morphology at Harvard University under the direction of Dr. E. C. JEFFREY, and I wish to express my thanks to him for his invaluable aid in the work and for the many courtesies extended to me during the year spent in his laboratory.

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EXPLANATION OF PLATES I, II

PLATE I

FIG. 1.—Transverse section of wood of stem of *Podocarpus totara*, $\times 250$.

FIG. 2.—Longitudinal radial section of wood of stem of same, $\times 250$.

FIG. 3.—Transverse section of wood of stem of *Cephalotaxus drupacea*, $\times 250$.

FIG. 4.—Same as fig. 3, $\times 40$.

FIG. 5.—Transverse section of wood of root of *Cephalotaxus drupacea*, $\times 250$.

FIG. 6.—Transverse section of wood of stem of *Torreya taxifolia*, $\times 250$.

PLATE II

FIG. 7.—Longitudinal radial section of wood of stem of *Torreya taxifolia*, $\times 250$.

FIG. 8.—Transverse section of wood of stem of *Taxus brevifolia*, $\times 250$.

FIG. 9.—Longitudinal radial section of wood of stem of *Taxus brevifolia*, $\times 250$.

FIG. 10.—Transverse section of wood of root of *Taxus cuspidata*, $\times 30$.

FIG. 11.—Upper portion of same, more highly magnified, $\times 125$.

FIG. 12.—Longitudinal radial section of wood of root of *Taxus cuspidata*, $\times 125$.